AN EXPERIMENTAL STUDY OF THE LIFE CYCLE AND ORGAN DIFFERENTIATION OF AURELIA AURITA LAMARCK

BULLETIN OF THE MARINE BIOLOGICAL STATION OF ASAMUSHI,
VOL. XV, NO. 3, 1975

AN EXPERIMENTAL STUDY OF THE LIFE CYCLE AND ORGAN DIFFERENTIATION OF *AURELIA AURITA* LAMARCK[1)]

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The life cycle of *Aurelia aurita* Lamarck and its alternation of generations have attracted the attention of many biologists since the early days of research in this field, and there are a number of descriptions on this species, although they are mostly fragmentary. The author has observed the natural life cycle of this species in Mutsu Bay, as well as the developmental cycle in the laboratory, from eggs to adult medusae and to the differentiation of gonophores. She succeeded in maintaining these organisms throughout the year by placing them under laboratory control for each developmental stage. As a result, the whole life cycle of this species has been clarified. Various new facts obtained through experiments on the problems of attachment, strobilation and ephyra differentiation will be described in this paper.

An effort has been made to avoid repeating descriptions that have been published previously. The drawings presented by Herourad (1909) has been reproduced with the additions of the author.

The photographs for Plate I, 1 and II, 18 were included through the courtesy of Dr. E. Hirai, for which the author expresses her sincere appreciation to him.

MATERIALS AND METHODS

From July to August 1957, a great number of *Aurelia aurita* appeared in the vicinities of Yuno-shima and Futago-shima in Mutsu Bay. As materials, 20 females of adult medusae were collected and fed with larvae of brine-shrimp in the laboratory to observe their life cycle. In the field, medusae, which appear in the waters near Asamushi every year, were observed and their behavior was recorded. This investigation, along with records on polyps collected on the sea corst and ephyrae caught with a plankton net, were used to study the life cycle of this species of jelly fish. Experiments were conducted on acceleration of the beginning of differentiation from the planula into the polyp, acceleration of the start of

1) Contributions from the Marine Biological Station, Tôhoku University, Aomori City, No. 416

strobilation, effect of temperature on differentiation from the strobila into the ephyra, and differentiation of the strobila by severance. Materials used for experimentation were obtained from the laboratory cultures.

OBSERVATIONS

I. Life cycle of Aurelia aurita in Mutsu Bay

This species seems to have made its first appearance in Mutsu Bay around 1954. According to a personal letter to the author from the late Dr. Seiji Kokubo (former head of Marine Biological Station, Faculty of Science, Tôhoku University), there had been no known record on its earlier presence in this area. In Japan, the number of jelly fishes which swarm in its coastal waters has been on the increase in recent years, and there are reports of damage to fishing nets and cooling water channels of water-front thermal power plants from swarming jelly fishes.

In Mutsu Bay, their appearance varies from year to year, they were very abundant from 1956 to 1960 and again from 1966 to 1969. In the Asamushi area, they are usually observed from June to November. By July or August, they grow to about 10 to 20 cm in diameter with some even reaching 30 cm in diameter. They occasionally drift to the shore in swarms. At maturity, the male is easily distinguished from the female because the male gonophore is white, that of the female is pink. By turning over the umbrella of a mature female, one will find oral lobe which contains a mixture of cleaving eggs and planulae in varying stages of growth. The embryos are all transparent and represent various stages of development. Likewise, the planulae include early stages larvae which are 180 μ in diameter, white, spherical organisms, more advanced larvae of light yellow color, and well grown larvae with attachment projections of yellowish brown and a body length of 200 to 250 or 300 microns.

However, during the winter months of January and February, medusae (about 15–20 cm in diameter) with relatively small planulae of 150 to 200 microns may sometimes be caught with a cod fishing net set at a depth of about 30 meters. Except for a record that in September 1968 Dr. M. Nishihira collected polyps attached to seaweed in Tsuchiya, the occurrence of polyps in the field has not been observed.

In the period from May to June 1960 and again in the same period of 1967, ephyrae were collected, a few at a time, with a plankton net. They have not been observed at any other period. In a year when jellyfish appear in large numbers, some change in their size apparently takes place sometimes in July. This phenomenon is observed when the sea is calm, but neither on rainy days nor immediately after rough sea. From early to late July, large-sized jelly fish disappear, even though they were present until the latter part of June, and in their place small jelly fishes of 1, 2, 3, 5 and 8 cm in diameter begin to appear in the surface water. They may form a mass as large as 10 meters in diameter. However, these small jellyfishes are again succeeded by swarms of large ones in August.

II. Developmental cycle in the laboratory

Formation of polyp from planula: Using a pair of scissors, gonophores and oral lobes were cut from female medusae which had been collected as specimens. After washing off slime with a pipette, eggs and planulae were transferred to petri dishes filled with sea water. The eggs were transparent and had a diameter of about 180 microns. They represented various stages of development, ranging from earlier stages to later. The planulae were also a mixture of larvae in varying developmental stages: the planulae of earlier stages were ovoid in shape, 180 microns in length and of an opaque, milk white color. Those of the intermediate stages were light yellow, pear-shaped and measured about 200 to 250 microns. The larvae of the advanced stages were yellowish brown and had attachment projections. Planulae which had been swimming in the oral lobe continued to be active in the petri dish. However, embryos in the early stages degenerated within a few hours after their transfer to the petri dish, whereas blastulae or gastrulae transformed into planulae by the following day. Planulae left in the petri dish became attached to either the bottom of the vessel or the surface of the water in 3–5 days, and differentiated into young milkywhite polyp with four tentacles. The number of tentacles doubled to eight in another 3–5 days. In seven to 10 days, these polyps grew to typical scyphistomes with a total of 16 tentacles. Young polyps which just completed differentiation from planulae were 200 to 240 microns in length with a slender stalk. Although they were initially in an inverted triangular form, they grew to light pinkish organisms of 500 microns to 2 mm in length with a thicker stalk after feeding on brine shrimp larvae. After 10 to 15 days, the polyps developed to a length of 25 mm, took on a cylindrical form with a rather broad hypostome, and began asexual reproduction.

Asexual reproduction of polyps: In the laboratory experiment, four types of asexual reproduction were observed. (1) The base of a well grown polyp gives rise to a stolon which swells at its tip. By the second day, the tip portion produces a four tentacle polyp. By the third day, the young polyp grows into a polyp with 16 tentacles and the stolon is separated from the parent. The polyp now becomes an independent unit. The growth of the stolon is retarded at a temperatures of 5 to 10°C but is promoted at temperatures of 20 to 25°C. Thus the distance between the young polyp and the parent varies, depending on the temperature conditions to which the stolon is exposed. Also, there are cases where a polyp buds from the middle part of a long stolon. (2) A young polyp grows out directly from the base of the body of the mother polyp. The outgrowth is eventually cut off to become an independent unit which attaches to the substratum at a position immediately next to the mother. (3) The polyp expands sidewise as though the opposite sides of the body are pulling against each other, thereby increasing the number of tentacles. When the number of tentacles reaches 20 to 30, the polyps is split longitudinally into two new polyps. (4) When a polyp moves from one location to

another, it may leave some of its tissues behind. A new polyp develops from these remaining tissues. When a stolon from a polyp has attached to the petri dish and has subsequently degenerated and been resorbed by the parent or has subsequently been retracted as the parent moves away, the pedal disk remaining on the petri dish produces a new polyp. The formation of a polyp from the pedal disk takes three to four weeks. However, when the pedal disk is kept at 2 to 5°C for two days, and then returned to room temperature a polyp is formed in about five to seven days. This indicates that low temperature treatment accelerates the formation of polyps.

In these four patterns of proliferation, the optimum temperature for acceleration of asexual reproduction was about 25°C. In case no feed was given for an extended period, large ployps fed on small ones around them and the number of individual units decreased. To maintain polyps without food, they should be kept at a low temperature (5–8°C). Since neither asexual reproduction nor canibalism takes place under such low temperature conditions, polyps survive without food for several months.

From strobilation to ephyra formation: When they are reared at room temperature, the activity of the polyps diminishes as the temperature drops in the autumn. Around October when the temperature fell to about 14–18°C, they became 25 to 30 mm in length and began to elongate further. The endoderm developed a zigzag pattern of transverse grooves, while the thickness of the ectoderm became uneven. Within several days after the hypostome had projected, signs of strobilation at the base of the tantacles in the tip of the polyp could be observed. A polyp which developed from the parent on August 6 proliferated to 129 units by October 7; i.e., in about two months. Of these, 38 units of more than one month old polyps began strobilating simultaneously. In one week thereafter, 10 days old polyps which were still linked to the mother polyps by their stolons also exhibited the formation of strobila. In petri dishes, the strobilation rate was 20 to 30% in the lowest groups and 70 to 80% in the highest. In petri dish was 100% strobilation recorded.

As regards the process of strobilation, on the first day one segment appeared below the tentacle rudiments and at the same time tentacles began to shrink. On the second day, two to three segments were observed; these became three to five on the third day. Thereafter, the number of segments formed increased according to the size of individual polyps, and the segmentation was completed by the fifth day. Around this time, every other tentacle shortened rapidly and thickened; at the same time, both sides of the tentacle base swelled and the rudiments of eight radial lobes began to form in each individual. Strobilation commenced from the tip of the polyp, leaving intact about one third of the column. When four to 18 segments were formed in each individual within four to 10 days after the beginning of strobilation, the eight tentacles which had been shrinking

were completely resorbed by the body to form rudiments of the radial lobes. The remaining eight tentacles also degenerated and were resorbed with a delay of one day. These eight tentacles disappeared between the radial lobes. After two days a groove developed in the central part of each radial lobe rudiment. At the base of this groove, a sensory organ was formed and ephyra lappets began to grow. Together with the first strobila, the fourth and fifth ones differentiated into ephyra rudiments. The other segments subsequently completed an ephyra one after another at intervals. Polyps at this stage may be 3–8 mm in length. In the case of the first segment, the differentiation from the strobila to the ephyra required seven to 10 days. However, segments that developed later completed their differentiation in five to six days. After all the segments had completed their strobilae, the tip of the tissues of the remaining polyp regenerated eight tentacles.

Six to 12 hours after the distal ephyra began to move, it was pulsating regulary, every two seconds, and separated from the mother polyp within 12 to 24 hours. Upon separation of all ephyrae, the polyp doubled the number of tentacles to 16. Cultured polyp began active asexual reproduction in two to three weeks. As they reached full size, the strobilae turned yellow and then brown. Continued provision of sufficient food after complete strobilation deepened their pigment and color. However, strobilae formed by rearing the parents in a dark room on meager food were white to light yellow in color with a little pigment.

Ehyra and metamorphosis: Ephyra which had just been cut off from the strobilae were yellowish brown and 2–3 mm in size. Each of the eight radial lobes bifurcated to form a total of 16 ephyral lappets. A sensory organ was located on the base of each ephyra lappet. The gastric cavity contained two gastric filaments in each of four locations. Except for the radial lobe, the structure was the stomach; the manubrium ran in its center with the tip of the mouth slightly open. After five to seven days, the ephyrae grew to 4–5 mm. At this stage, the muscles with ephyra lappets began to project between radial lobes, continuing from the subumbrella above the gastric cavity, the mesoglea of the umbrella became thick and the number of nematocysts increased. After 10 to 15 days of rearing, they grew to 6–7 mm. The ephyra lappets of the radial lobes expanded and the muscles which began to extend between the radial lobes reached about 1/2 of the length of a radial lobe. The center of the mesoglea further thickened and the manubrium also increased to 3–5 mm in length.

The gastric filaments increased to 4–5 at each site. In the meanwhile, the radial lobes became slender and tubular. The coelenteron began to have partitions forming four lobes in the base of the manubrium. With the lapse of 21 to 27 days, the ephyrae grew to about 10 mm and the muscles developed to the full length of the radial lobes to form an umbrella. The cruciform base of the manubrium began to be separated into four parts to undergo differentiation into oral lobes. The coelenteron differentiated into four gastric lobes. In 30 to 35 days,

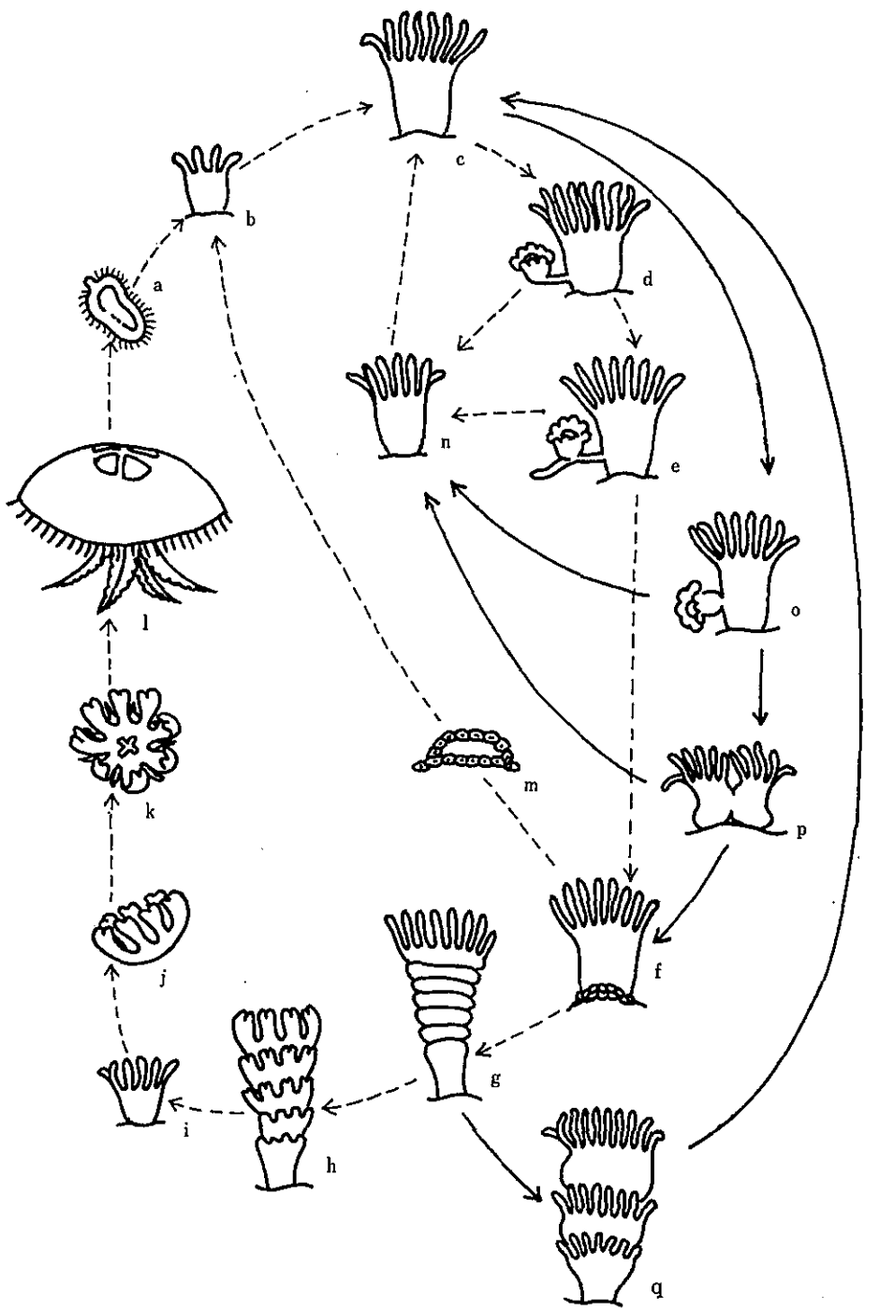

Fig. 1. Life cycle of *Aurelia aurita*: Herouard's drawing of developmental cycle (broken line) (Uchida '57) supplemented by the author (thickline)
a-l: Ordinary developmental cycle c-q: Asexual reproduction
Others: Developmental cycles obtained from experiments.

the ephyrae grew to 12 mm, and the radial lobes and central part of the developed muscles differentiated into a total of 16 inter-radials and ad-radials. Along the margin of the umbrella, the ring canal and the velum were formed and the rudiments of tentacles began to appear. The digestivetract, or the intervascular system, was pink, the sensory organ yellowish orange and the ocellus red. In this way, in about one month of rearing, the ephyrae developed into young medusae of the smallest size, undergoing metamorphosis as in the case of formation in nature of matured medusae of *Aurelia aurita*. Thereafter, the radial canal forked into per-radial canals, the intervascular system became complicated and narrow creases emerged in the margin of the oral lobe. About three months later, when the medusae had grown to 35–50 mm in size, they became mature, each forming four pieces of the gonophore around the gastric lobe (Fig. 1.).

III. Experimental observation on differentiation in asexual reproduction stage

I. Experimental study on relations between attachment and differentiation

a. *Differentition from planula to ephyra*

Planulae obtained from adult medusae were placed in petri dishes either as such a large population that the organisms were in contact with one another, or without washing off the mucus of the radial lobes. In either case, two days later they attached to the bottom of the petri dish. Subsequently, about 90% of the planulae differentiated into an ephyra with a peduncle, skipping the polyp stage, whereas 5% developed into a polyp provided with one ephyra at its tip. The remaining 5% differentiated into a polyp alone. This fact proves that the planula

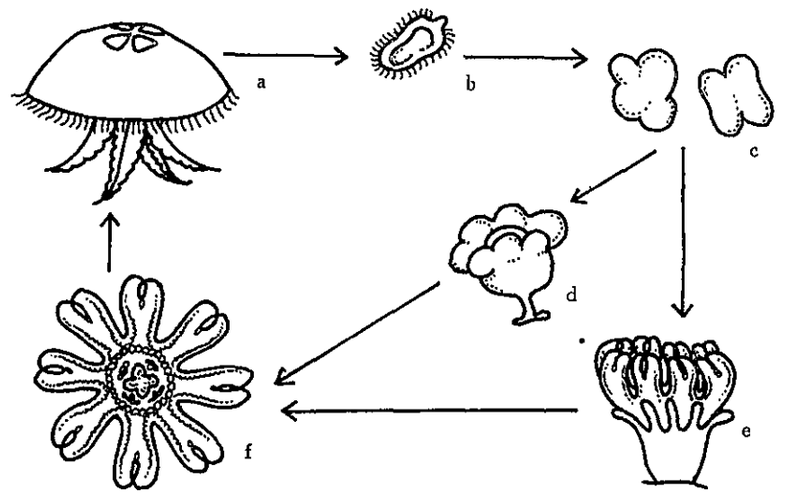

Fig. 2. Development of *Aurelia aurita* which does not undergo the alternation of generations. The planula attached to the substratum and directly differentiated into the ephyra, skipping the polyp stage.

possesses the ability to differentiate into either of the two forms – polyp or ephyra – depending on the given conditions. Haeckel (1881) had already noted, and more recently Hirai (1958) reported that the planula can differentiate into the ephyra without having the alternation of generation. However, neither of these authors indicated that this pattern of differentiation took place at a high percentage in their respective observations (Fig. 2.).

b. Attachment of planulae

In a petri dish containing planulae, a narrow piece of brown seaweed was introduced. Within about one hour, planulae attached to the strip and the initiation of differentiation into polyps was accelerated by this attachment, suggesting that attaching to the substrate may be a prerequisite for a planula to differentiate into a polyp. As the next step, the following experiment was conducted to determine whether or not it is a necessary condition of differentiation for a planula to remain attached to the substrate. About 100 planulae were introduced into a petri dish which contained a narrow pieces of brown seaweed, and about one hour later those specimens which had attached to the seaweed were separated from the substratum with a steel needle. Although the time required for attaching varied, they still had the external appearance of planulae. Of detached planulae, 20% again attached to the bottom of the vessel, while 30% began a slow movement by means of their cilia. The other 50% settled on the bottom in the detached state. Another hour later, the moving planulae continued to be detached and all of them formed tentacle rudiments while moving. When the hypostome and tentacles began to develop, they attached to the bottom of the petri dish. This fact suggested that a planula does not need to be in the state of attachment when differentiation into a polyp takes place. Even if it is in motion, it will apparently undergo differentiation once it has received a stimulus in the form of brief attachment.

2. Acceleration of strobilation

In 1961 to 1962, the author conducted experiments on methods to accelerate the initiation of strobilation *Aurelia aurita* (Kakinuma, 1963). Subjecting polyps to a temperature of 15°C and lighting of 5000 lux led to 100% strobilation in the season when strobilation is considered to take place in the field. Strobilation was also successfully induced at a high rate over 80% in a season when polyps in field are unlikely to strobilate. Thus, the author succeeded in producing ephyrae from polyps in the laboratory at any time throughout the year.

3. Effect of temperature variation on differentiation from strobila into ephyra

a. Effect on strobilation in early stage

In the case of polyps which commenced strobilation at a temperature of 10 to 15°C and were still in its early stages where their ephyra rudiments were yet

to form radial lobe rudiments, sharp temperature variation (to a high temperature of 25°C and to a low temperatures of 2–5°C) inhibited differentiation into ephyrae at both low and high temperatures. Instead, each segment differentiated into a polyp which was later separated as a complete individual unit. In other words, when it was subjected to a sharp temperature change, regardless of whether to a low temperature or to a high temperature, the polyp would not differentiate into an ephyra even after a strobila had already been formed.

b. Effect on strobilation in advanced stage.

Strobilae in the advanced stages where the rudiments of radial lobes had already been formed, did not reprogress to polyps when they were exposed to the sharp temperature change. When they were placed at a high temperature of 25°C, strobilae advanced the separation of ephyrae by about two days as compared with the control. Strobilae which were placed under low temperature conditions (2–5°C) failed to separate their ephyra. After about 10 to 14 days, these strobilae cut off deformed ephyrae, often with shrunken ephyra lappets. Differentiation of the ephyra was accelerated in the strobilae under high temperature conditions while it was retarded in the strobilae under low temperature conditions. No differentiation was observed in any other organ. Based on this experimental results, it is considered that, in the developmental process of a polyp to a strobila and then to an ephyra, there is a borderline that determines whether the strobila reverts to a polyp or differentiates an ephyra when exposed to a radical temperature variation. It is presumed that this borderline is the time that the segments in the strobila develop into radial lobe rudiments.

4. Strobilation by abscission

The segments of twenty polyps in the advanced stages of strobila formation were separated from the parent polyp by cutting. After two days at 20°C, these segments became free swimming ephyrae. Polyps in the early stages of strobilation, including those in the process of forming the radial lobe rudiments, those with the radial lobe rudiments yet to grow out and those which had completed segments only, all differentiated into complete ephyrae at 20°C two days later. However, only the largest endmost ephyra on the body, which was 4 mm in diameter, made movements, while the other polyps were small (2–2.5 mm) and showed no movement at all. The part which was lying below the strobila and which had no segments became an incomplete ephyra or a deformed one with 5–7 ephyra lappets. Strobilae with fewer ephyra lappets became polyps. From this experiment, it was found that, while the controls with their strobilae of the later stages left in place required three to four days to differentiate into ephyrae when they were left at room temperature, separated from the parent body by cutting became slightly small but otherwise complete ephyrae in two days, indicating the acceleration of differentiation by severance. Even if a strobila in its early

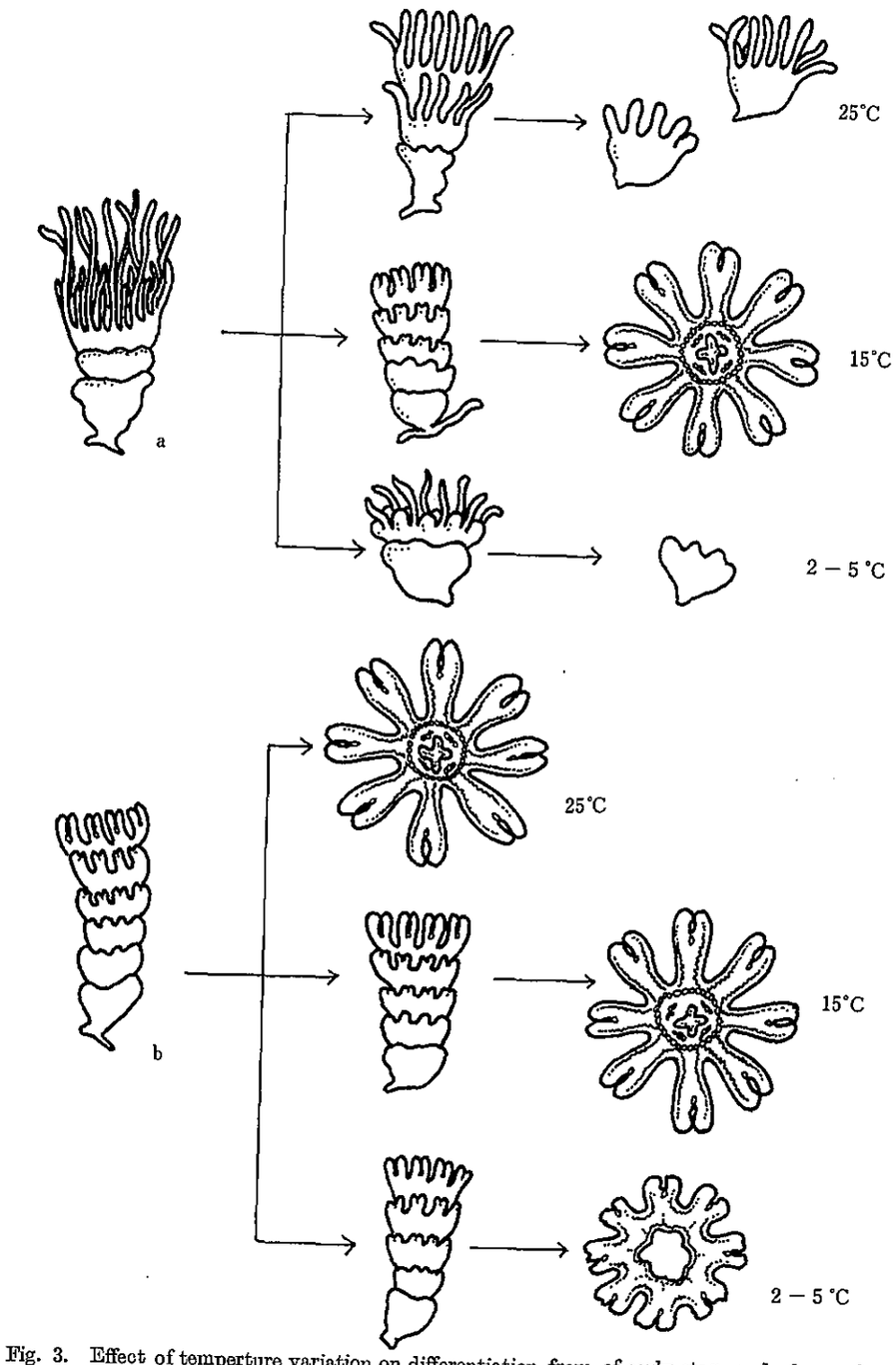

Fig. 3. Effect of temperture variation on differentiation from of early stage and advanced stage strobila into ephyra.

stages where segmentation had just begun was cut off, the isolated pieces metamorphosed into complete ephyrae. This metamorphosis was completed in two days after severance as in the case of differentiation of amputed strobilae in advanced stages. This is in sharp contrast to intact strobilae in advanced stages which needed five to seven days to differentiate into ephyrae. From this fact, it was found that in the process of developing from polyp to strobila and strobila to ephyra, differentiation of strobila into ephyra has already been programmed once the segments have emerged in the polyp, and also that the severance of segments will not cause them to revert to the polyp stage, but will rather accelerate differentiation into the ephyra, which is further promoted by a rise in temperature. Based on this fact, it is postulated that the strobilizing polyp has two capacities – one is to revert to an ordianary polyp and the other is to differentiate into an ephyra. Both capacities are considered to be balanced by maintaining correlation between them. Consequently, it is assumed that if one of these capacities is either supressed or stimulated, differentiation in either one of the directions will be accelerated at the expense of the other (Fig. 3).

5. Effect of attachment on regeneration of polyps

A number of polyps were ground into particles with a homogenizer and then filtered with Müler gauze Nos. 15, 25 and ultra XXIII. Each of the filtrates obtained with the three kinds of filters was left in a petri dish after diluting it with sea water. On the following day, small pieces of tissue in all these filtrated had cohered into several masses of nearly the same size. These masses were in the shape of a "confit" or a multi-pointed figure. On the second day, these masses became spherical and began movement by means of cilia. Some of these cell masses were left undisturbed others were put into an agitator which was then slowly rotated without interruption so that they would not attach to the surface of container. After seven to eight days, of the cell masses which had been left undisturbed in the petri dish, one third (masses of relatively large size) developed tentalces and formed polyps. The individual units which had grown into polyps could be divided into those which had attached on the bottom of the vessel and those which failed to attach. By the 10th day, tentacles had been grown on all the masses. However, the cell masses which had been stirred in the agitator were completely disintegrated within three to five days. It could not be determined whether this was because the cell masses had not been firmly formed or because they had not initiated differentiation. Therefore, the following experiment was conducted: Cell masses were left undisturbed for five days and from the sixth day they were slowly agitated. These masses failed to differentiate into polyps even in 10 to 12 days. In contrast, masses which had been left completely undisturbed all transformed into polyps in seven to 10 days as in the case of the earlier experiment. On the 13th day, since two thirds of the masses in the agitator had dis-

integrated, the surviving masses were left undisturbed thereafter, and differentiated into polyps in two days.

This experimental result led to an assumption that the differentiation from a cell mass into a polyp will not occur when the mass is kept suspended in water without contacting with any object. It was postulated that differentiation may take place even if the mass is not securely attached to the substratum so long as it is least in contact with some object. In other words, it is presumed that the differentiation of organs from a cell mass may require a stimulus to the initiation of such differentiation; a stimulus which is given to the mass when it contacts with some object.

SUMMARY

The life cycle of *Aurelia aurita* Lamarck has long been known to include an alternation of generations. However, no publication has so far been available which describes the entire life cycle of this species. The author collected embryos in various stages of development from mature female medusae at the Marine Biological Station of Asamushi, Tôhoku University. At the laboratory, she maintained and fed polyps which has been differentiated from these embryos. She successfully placed each stage of their development under laboratory control. With the use of these materials, observation was made on the developmental cycle of this medusa species. This covered the growing period from the egg to ephyra through the intervening stages of the planula, polyp and strobila, then metamorphosis into the adult medusa and development into the sexually matured one with the gonophore. Along with this laboratory investigation, its life cycle in field was observed. Since the process of normal growth in the life cycle is rather well known from early days of research on this species, the results of the current study fundamentally provide nothing particularly new. However, it is believed that the fact that one of the patterns of asexual reproduction observed involved fission is a new finding. A life cycle of this kind offers a variety of embryological problems to the researcher. Among these problems, the author dealt with the following in the present experiment to analyze the differentiation of organs in the life cycles of *Aurelia aurita*: the attachment of planulae, its effect on the differentiation from planula to polyp, conditions for contact with the substratum in regeneration from fragments of the polyp, acceleration of beginning of strobilation, and differentiation from the strobila into the ephyra.

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Explanation of Plate III~VI

Plate III.

1. Adult medusae of *Aurelia aurita* as they swarm near the shoreline.
2. Planulae just released from the gonophore.
3. Planulae which remain attached to a piece of seaweed and have formed the coelenteron and tentacle rudiments.,
4,5. Young polyps with eight tentacles which have differentiated upon attachment of seaweed.
6. Scyphistomae with 16 tantacles.
7. Growth of a new polyp from the tip of each of four stolons which extend from the parent polyp.
8. Multiplication of polyps by fission.
9. Budding of a polyp in the middle of stolon

Plate IV.

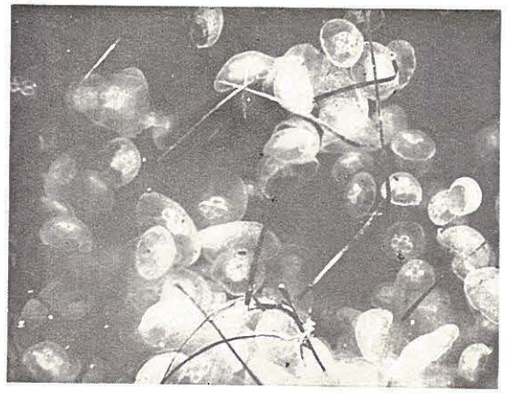
10. A polyp extends its mouth and tentacle toward food as it senses the approaching food.
11. The polyp catches the food.
12. The polyp retracts its tentacles after they have fully taken the food.
13, 14. Polyps in strobilation stages. The body extends into a moter-like shape with formation of wrinkles in the endoderm.
15. Polyps in strobilation, 1st day.
16. Polyps in strobilation, 3rd day.
17. Polyps in strobilation, 5th day. Every other tentacle shrinks and 16 tentacels are reduced to eight as a result.
18. Polyps and strobilae suspended from a glass plate.

Plate V.

19. Strobila on the verge of cutting off an ephyra.
20. Formation of polyps after releasing ephyrae.
21. An ephyra just released from the parent.
22. Free-swimming ephyrae.
23, 24.. Process of differentiation from planula directly into ephyra; Side view (23) and oral view (24).
25. Upon attachment, one planula formed an ephyra with a stolon and another formed a polyp and then an ephyra on top of the polyp.

Plate VI.

26. An ephyra with a stolon was completely differentiated from a planula.
27. An ephyra which is attached with its stolon and is ready to swim away.
28, 29. After about three weeks of rearing, ephyrae of *Aurelia aurita* grew to 8 mm medusae with the same form as that of the adult.
30, 31. Medusae after about 1.5 to 2 months of rearing.
32. Medusae in about 2.5 months of rearing.
33. Medusae in about 3 months of rearing (adult *Aurelia aurita*).



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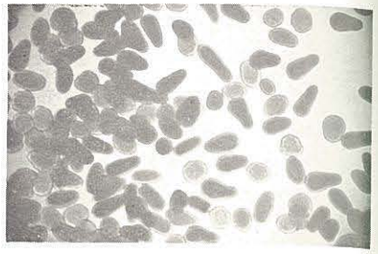

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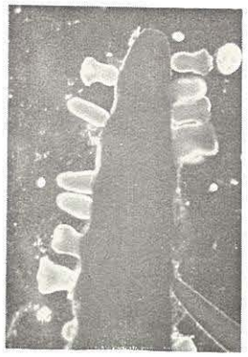

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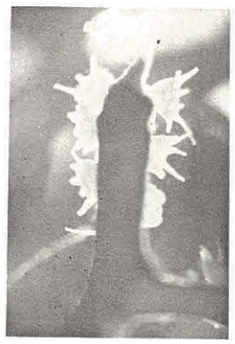

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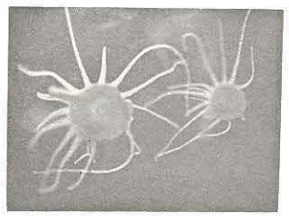

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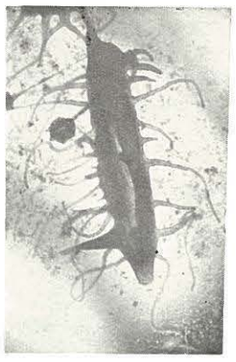

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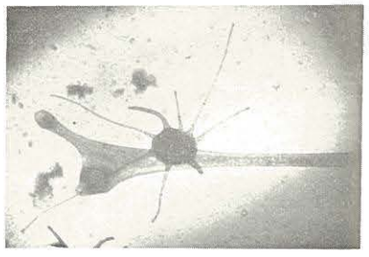

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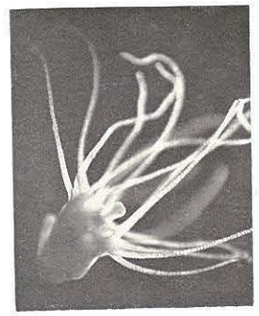

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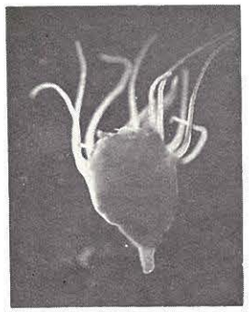

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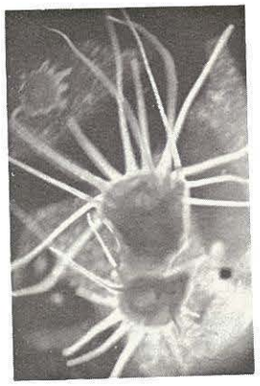

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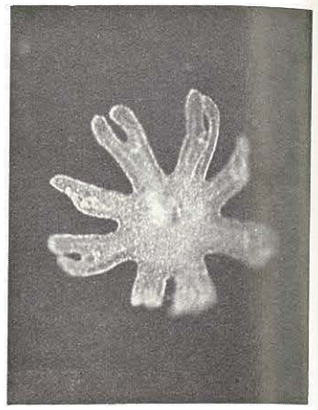

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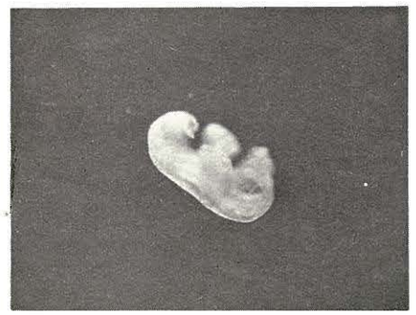

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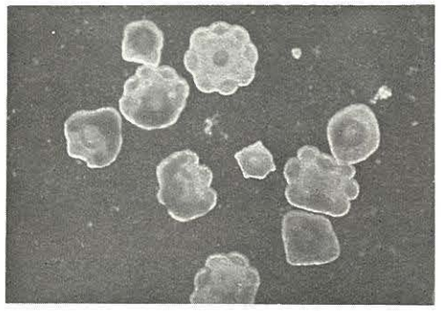

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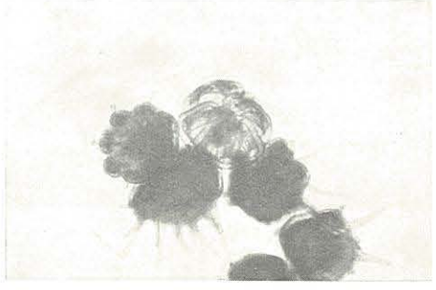

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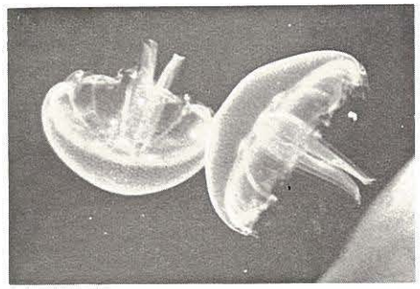

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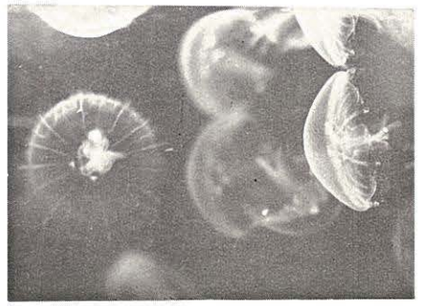

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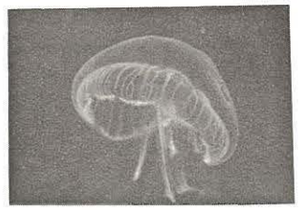

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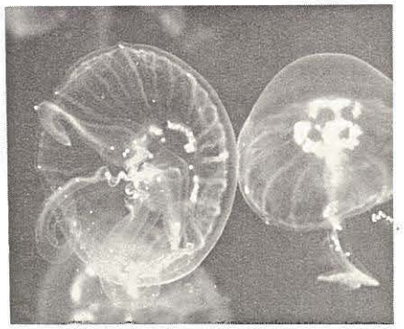

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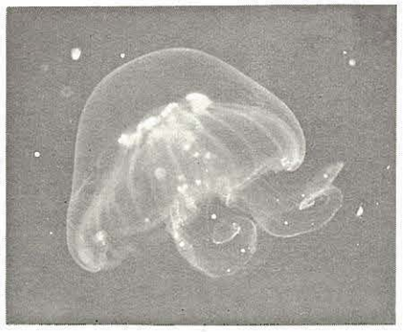

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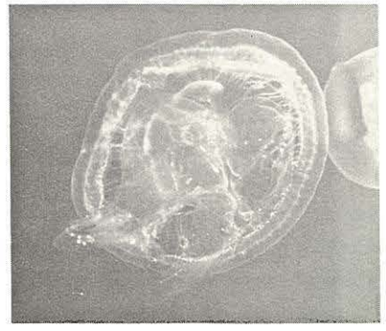

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